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VEGETATION RELATIONSHIPS AND FOOD OF SAGE SPARROWS WINTERING IN HONEY MESQUITE HABITAT

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The breeding habitat and behavior of Sage Sparrows (*Amphispiza belli*) have been documented by a number of investigators (Linsdale 1938, Miller 1968, Feist 1972, Rotenberry and Wiens 1978, Rich 1980). Although the breeding season is important to birds, conditions on wintering grounds may have a primary role in regulating populations of migratory species such as the Sage Sparrow (Fretwell 1972). Previously published information concerning wintering Sage Sparrows consists of general comments on distribution, habitat and food (Goss 1881, van Rossem 1911, Miller 1968).

Sage Sparrows usually arrive in the lower Colorado River valley during September and remain until February or early March. The species occurs in most riparian habitats, but the greatest number of sparrows is consistently found in vegetation dominated by honey mesquite (*Prosopis glandulosa*). Within honey mesquite habitat, Sage Sparrows tend to concentrate in certain areas.

Our primary purpose in this study was to identify aspects of riparian vegetation that consistently attracted Sage Sparrows. We did this by examining annual and seasonal variation in distribution of the Sage Sparrow population in the lower Colorado River valley. We also examined food use to determine if there were associations between Sage Sparrows and specific types of resources.

We found that presence of inkweed (*Suaeda torreyana*) characterized areas where the number of Sage Sparrows was greater than the average for all areas. To test the relationship of Sage Sparrows and inkweed, we planted three sites with different densities of inkweed and other shrubs. Evidence from these sites supports the conclusion that inkweed is actively selected by wintering Sage Sparrows.

METHODS

As part of a project evaluating wildlife use of riparian habitats, we established 72 transects (800 or 1600 m long) in representative riparian vegetation along the lower Colorado River from the Mexican border north to Davis Dam, on the Nevada-Arizona border. The transects covered the ranges of vegetation composition and vertical configuration present in the area. Each transect was placed in a relatively homogeneous stand of vegetation. General habitat types were identified by the dominant tree or shrub (if there were no trees) present in the stand. These habitats included screwbean mesquite (*Prosopis pubescens*), cottonwood (*Populus fremontii*)-willow (*Salix gooddingii*), salt cedar (*Tamarix chinensis*), honey mesquite, arrowweed (*Tessaria sericea*) and salt cedar-honey mesquite. Twenty of the transects were in honey mesquite vegetation in a 6000-ha area between Parker and Ehrenberg, Yuma Co., Arizona. All transects were censused two or three times per month using a modification of the Emlen (1971) variable distance method. Sage Sparrow data were collected between September and February each year from 1975–1980. Computer simulation has indicated that 6–9 censuses are necessary to obtain accurate population estimates (Engel-Wilson et al. 1981), so we considered "seasonal" data when making calculations such as distributional diversity and correlations of bird densities with vegetation variables. The fall season included September through November; winter included December through February. Seasonal densities of Sage Sparrows are the average of all censuses in each period.

Sage Sparrow distributional diversity among the 20 honey mesquite transects was calculated using $H = -\Sigma p_i \log_{10} p_i$, where p_i is the proportion of the total number of Sage Sparrows occurring on each transect (densities standardized to 40 ha). The extent to which the sparrows were equally abundant on all transects (evenness) equalled the proportion of maximum possible H ($H/\log_{10}N$, where N = total number of transects). Significance of differences in H was tested following Zar's (1974) method for diversity indices.

All trees and shrubs within 15 m of both sides of each transect were counted; densities were extrapolated to number per ha. Foliage indices, including foliage density (DEN), patchiness (PI) and foliage height diversity (FHD) were derived from measurements obtained with the board technique (MacArthur and MacArthur 1961). Our patchiness index represents the variance (S^2) associated with foliage density in 150-m units along each side of a transect. Further details of vegetation measurement techniques are available in Anderson et al. (1977, 1978). Initial vegetation measurements made in the summer of 1975 were used to characterize the vegetation available to Sage Sparrows in the falls and winters of 1975–76 and 1976–77. Measurements were repeated in summer 1977 and 1979; these values were used in examining Sage Sparrow habitat relationships in the subsequent falls and winters. We felt that it was valid to use vegetation measurements taken in one year to characterize the transects for several subsequent years because there was little change in most vegetation measurements between years. For example, not a single measurement taken in 1979 differed significantly from those for 1977. Measurements made on green foliage in summer reflect the density of nondeciduous foliage and/or leaf-bearing twigs in winter (Anderson and Ohmart, unpubl.). Vegetation variables considered in analyses included density of honey mesquite trees, densities of *Atriplex* spp. and inkweed shrubs, foliage DEN 0–0.6 m, total foliage DEN, PI 1.5–3.0 m, total PI and FHD. We chose these variables because they were not highly intercorrelated and described features of the vegetation that varied between transects.

A 2-tailed *t*-test tested differences in mean vegetation measurements between transects where Sage Sparrows occurred in below- and above-average numbers. Stepwise multiple regressions examined specific Sage Sparrow vegetation relationships. Data were transformed using square roots or $\log_{10}(N + 1)$ (Sokal and Rohlf 1969). Standardized vegetation variables were raised to the second, third and fourth powers in order to discern certain nonlinear functions that may be more appropriate for describing ecological relationships than simple linear functions (Green 1979; Meents et al., unpubl.). Regressions were terminated when additional significant variables accounted for $<5\%$ of the variance.

An index to relative insect biomass was obtained by weighing insects captured in a 4000-sweep sample on a transect in each habitat. The same transect was sampled in each habitat type each month in 1976 and 1977.

Three sites in the riparian floodplain of the lower Colorado River were manipulated to test the effect of changing the amount and structure of vegetation. None of these sites was used by Sage Sparrows prior to manipulation. Two areas (20 and 30 ha) were originally sandy dredge spoil that supported little vegetation. A third site (20 ha), originally covered by salt

TABLE 1
AVERAGE CHARACTERISTICS OF SAGE SPARROW POPULATIONS AND DISTRIBUTION ON HONEY MESQUITE TRANSECTS

	1975–76		1976–77		1977–78		1978–79		1979–80	
	FA[a]	WI[b]	FA	WI	FA	WI	FA	WI	FA	WI
$\bar{x}$ density	2.7	5.3	4.3	6.5	5.5	7.0	8.2	7.9	16.5	12.6
SE	±0.9	±3.5	±1.9	±3.9	±1.8	±2.9	±2.7	±3.8	±4.3	±2.8
Evenness	0.67	0.28	0.58	0.43	0.76	0.66	0.73	0.59	0.82	0.85
H	2.01	0.85	1.74	1.28	2.26	1.98	2.17	1.77	2.44	2.52
H change[c]	$P < 0.001$		$P < 0.01$		$P < 0.05$		$P < 0.001$		NS	

[a] FA = fall.
[b] WI = winter.
[c] Significance of difference in H between seasons (Zar 1974).

cedar, was cleared. All three areas were revegetated with native trees and shrubs, including cottonwood, willow, honey mesquite, palo verde (*Cercidium floridum*), wolfberry (*Lycium pallidum*), quail bush (*Atriplex lentiformis*) and inkweed (Anderson et al. 1978). Site I had no inkweed, site II had a small amount of inkweed and site III had a high density of inkweed. All areas were censused during fall 1980 and winter 1980–81.

RESULTS

Birds.—The average annual density of Sage Sparrows in honey mesquite habitat showed a gradual increase over the 5 years of study (Table 1). Mean densities increased from 2.7 birds/40 ha in fall 1975 to 16.5 birds/40 ha in fall 1979. A less dramatic increase occurred from winter 1975–76 (5.3 birds/40 ha) to winter 1979–80 (12.6 birds/40 ha).

Densities of Sage Sparrows in all other riparian habitats were very low between fall 1975 and winter 1978–79 (all habitats were not censused in 1979–80). Average densities for the 4 years were 0.28 (SE = ± 0.18) birds/40 ha in fall and 0.06 (SE = ± 0.03) birds/40 ha in winter. Because of these low densities only honey mesquite habitat was considered in further analyses.

Some transects regularly supported higher densities of Sage Sparrows. Five transects had above-average Sage Sparrow numbers in at least 2 years in fall; three of these were above average in all 5 years. In winter, four transects had above-average densities in at least 2 years; two of these were preferred in all 5 years. Two transects were above average in both seasons during all the years sampled.

Both distributional diversity and evenness of Sage Sparrows were reduced from fall to winter of each year, except in 1979–80 when differences between seasons were not significant (Table 1). This indicated that the sparrow population became concentrated in a few areas as winter progressed.

In 1979–80, when distributional diversity and evenness were greatest, sparrow numbers were higher than in any previous year (Table 1). Densities in this year were above average on a number of transects where only below-average densities had occurred previously. This was especially apparent during winter. However, transects that had been consistently favored in previous years continued to support high densities of Sage Sparrows.

Vegetation.—The only statistically significant difference in vegetation between transects with above- and below-average densities of Sage Sparrows was in the number of inkweed shrubs (fall $P < 0.001$, winter $P < 0.01$). Inkweed in the lower Colorado River valley occurs primarily in patches within areas dominated by honey mesquite. Sage Sparrows also tended ($0.1 > P > 0.05$) to be absent from transects with high densities of honey mesquite trees and *Atriplex* spp. shrubs.

Seasonal vegetation relationships were examined with stepwise multiple regressions of Sage Sparrow numbers against all vegetation variables. Overall, relationships with the vegetation accounted for an average of 68% of the variation in Sage Sparrow densities (Table 2). Inkweed density was the first variable selected in 9 of 10 cases. Inkweed density alone accounted for an average of 50% of the variance and always showed a positive relationship with Sage Sparrow densities. The relationship was linear in only one case. Half of the times when inkweed was included as a significant step the square of inkweed density was chosen. When graphed, this produced a U-shaped curve, indicating that Sage Sparrows occurred on some transects that had no inkweed and were present in relatively low numbers on some transects that had intermediate densities of inkweed. The cube of inkweed density was included in three cases. This indicates a near-linear relationship between inkweed and Sage Sparrow densities, but some transects that had inkweed had a rather low number of Sage Sparrows.

The second variable chosen in the stepwise regression procedure was different between seasons (Table 2). Densities of honey mesquite and *Atriplex* spp. shrubs showed negative relationships; foliage patchiness and density measures had positive relationships with sparrow densities.

The reduction of sparrow distributional diversity between fall and winter was not paralleled by any consistent change in association with vegetation. Inkweed was the most important habitat component in both seasons.

Sage Sparrow densities varied among the three revegetated sites (Table 3). The areas that had little or no inkweed supported similarly low sparrow densities in both seasons ($\bar{x} = 2.8$ birds/40 ha). The area with a relatively

TABLE 2

SUMMARY OF STEPWISE MULTIPLE REGRESSIONS BETWEEN SAGE SPARROW DENSITIES AND HONEY MESQUITE VEGETATION VARIABLES

Year/season	Vegetation variables[a] Step to enter 1	2	3	4	Total R^2
1975–76					
Fall	inkweed[2]	-mesquite[4]	FHD[3]	DEN 0–0.6[4]	
	0.34	0.07	0.16	0.05	0.62
Winter	inkweed[3]	PI sum[4]			
	0.67	0.05	—	—	0.72
1976–77					
Fall	inkweed	-*Atriplex*[4]			
	0.72	0.10	—	—	0.82
Winter	inkweed[4]	-*Atriplex*			
	0.66	0.09	—	—	0.75
1977–78					
Fall	inkweed[3]	PI sum[4]			
	0.40	0.10	—	—	0.50
Winter	inkweed[2]	PI 1.5–3[4]			
	0.62	0.06	—	—	0.68
1978–79					
Fall	inkweed[2]	-mesquite	-mesquite[4]		
	0.41	0.23	0.10	—	0.74
Winter	inkweed[2]				
	0.73	—	—	—	0.73
1979–80					
Fall	-mesquite	inkweed[2]	DEN 0–0.6		
	0.35	0.19	0.06	—	0.60
Winter	inkweed[3]	-DEN sum	-DEN sum[4]	PI 1.5–3[4]	
	0.21	0.17	0.14	0.09	0.61
Mean R^2					0.68

[a] Numbers below variables are R^2 for the first step and R^2 change for subsequent steps.

high density of inkweed also had a high density of Sage Sparrows ($\bar{x}$ = 46.5 birds/40 ha).

Diet.—Insect biomass in riparian habitats of the lower Colorado River valley showed seasonal cycles of abundance (Fig. 1). Insect biomass declined throughout late summer, fall and winter; a similar pattern occurred in honey mesquite habitat.

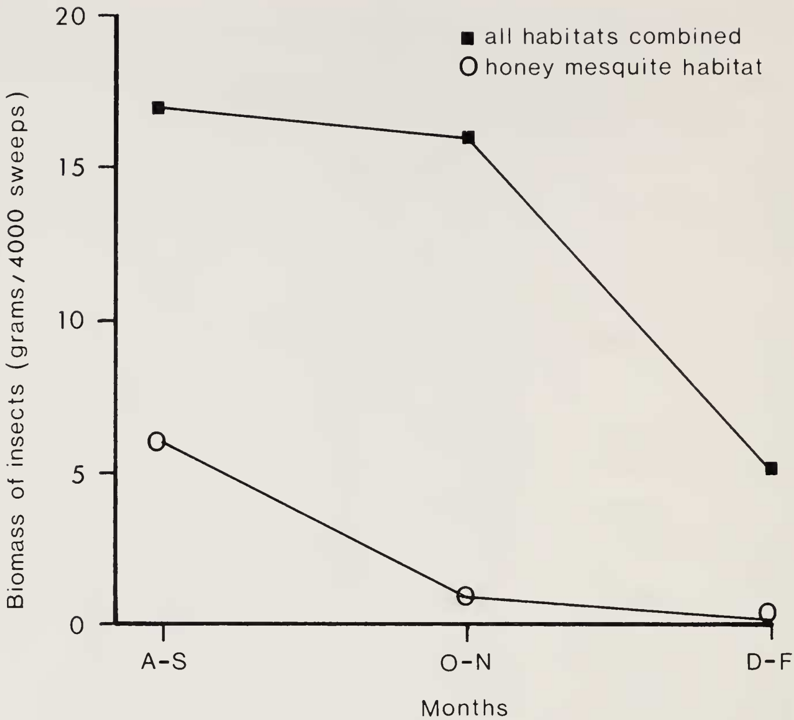

FIG. 1. Average insect biomass in riparian habitats of the lower Colorado River valley; A–S = August–September, O–N = October–November, D–F = December–February.

Analysis of gizzard and esophageal contents of Sage Sparrows collected in honey mesquite habitat also indicated seasonal changes (Table 4). In fall, animal material constituted an average of 44% of the volume of sparrow stomach contents; the remaining 56% was seed and plant material.

TABLE 3

DENSITIES OF *ATRIPLEX LENTIFORMIS*, INKWEED AND SAGE SPARROWS ON THREE MANIPULATED SITES

	Shrubs (no./ha)		Sage Sparrows (no./40 ha)	
Site	*Atriplex*	inkweed	fall 1980	winter 1980–81
I	7.6	0.0	3.5	2.7
II	40.0	0.8	2.0	3.0
III	134.0	23.9	30.5	62.0

TABLE 4
RESULTS OF STOMACH ANALYSES OF SAGE SPARROWS COLLECTED IN HONEY MESQUITE HABITAT

Season	N	Material	% occurrence[a]	% volume[a]
Fall	8	Coleoptera	28.4	17.7
		Hemiptera	7.8	9.1
		Homoptera	3.9	1.1
		Orthoptera	3.9	1.7
		Formicidae	14.3	6.4
		Unidentified insect	3.9	8.4
Subtotal			62.2	44.4
		Chenopodiaceae seed	7.8	5.2
		Unidentified seed	3.9	3.3
		Unidentified plant	26.0	47.2
Subtotal			37.8	55.7
Winter	12	Coleoptera	4.2	1.3
		Homoptera	2.1	0.8
		Lepidoptera	2.8	5.6
		Formicidae	7.7	2.5
		Unidentified insect	10.8	2.5
Subtotal			27.5	12.7
		Chenopodiaceae seed	3.8	0.5
		Unidentified seed	11.5	4.2
		Unidentified plant	55.0	81.3
Subtotal			70.0	86.0
		Feather	2.1	1.3

[a] Columns do not add to 100.0 because of rounding.

Stomach contents of Sage Sparrows collected in winter had only 13% animal material; the rest consisted mostly of plants and seeds.

DISCUSSION

The gradual increase in the Sage Sparrow population over the 5 years of study was part of a general trend observed for many avian species in the lower Colorado River valley (Anderson and Ohmart, unpubl.). This increase was apparently related to the series of relatively mild winters and favorable food resources that followed the particularly severe winter of 1974–75. The population increase could also have been due to increased breeding success or resource or climatic conditions in other parts of the Sage Sparrow range that resulted in more birds wintering in the lower Colorado River valley.

Sage Sparrows occurred in honey mesquite habitat more frequently than in other riparian habitats. As has been shown, this relationship was incidental since Sage Sparrows were associated with inkweed, which in the lower Colorado River valley occurs mostly in honey mesquite habitat. Site III of our vegetation manipulation study had high densities of inkweed and Sage Sparrows, but essentially no honey mesquite because at the time of this study, newly planted trees were <1 m tall and contributed minimally to the vegetation.

The observed distribution restriction between fall and winter and the overall association with inkweed may be explained by at least two nonexclusive alternatives. Sage Sparrows are almost exclusively insectivorous on their sagebrush (*Artemisia* spp.) breeding ground (Wiens and Rotenberry 1979) and the wintering population in the lower Colorado River valley consumed proportionately fewer insects throughout fall and winter. These seasonal changes were probably related to reduced insect availability accompanying the onset of winter. Incidental behavioral observations showed birds frequently feeding near or under inkweed. The shift to vegetation and seeds as primary food sources when there was a restriction of Sage Sparrows to inkweed areas suggests that inkweed is an important food in winter. Weather was mild in the one winter (1979–80) when sparrows did not show distribution restriction from fall to winter. Mild winters in the lower Colorado River valley have higher insect populations than harsh winters (Anderson and Ohmart, unpubl.). Abundant food resources and moderate temperatures may have allowed Sage Sparrows to winter in previously unsuitable areas.

Fretwell (1972) suggested that migratory birds may benefit if they winter in habitats resembling their breeding grounds (or choose breeding habitat that is similar to winter habitat, if winter conditions limit population size). Winter experience in inkweed areas may enhance reproduction and/or survival of Sage Sparrows on their structurally similar sagebrush breeding grounds (or vice versa). However, Sage Sparrows were not found in significant numbers in other vegetation of physiognomy similar to sagebrush. In particular, sparrow densities on honey mesquite transects and manipulated sites did not show a positive relationship with *Atriplex* spp. shrubs, so general structural features alone are apparently not responsible for the distribution of Sage Sparrows in their winter habitat.

Although there was clearly an association between Sage Sparrows and inkweed, this relationship was not simple, as evidenced by the selection of nonlinear variables in the regressions. It is unlikely that sparrows respond to only one aspect of their habitat, and their association with inkweed is undoubtedly modified by other factors. Some transects with inkweed also had high densities of honey mesquite and *Atriplex* spp. shrubs; both of these are apparently avoided by Sage Sparrows. These transects account for the lower than expected number of Sage Sparrows on some transects that had inkweed.

The appearance in 1979–80 of above-average numbers of Sage Sparrows on transects that did not have a significant amount of inkweed supports the model of habitat selection and distribution proposed by Fretwell and Lucas (1969). According to this model, at low total population size only the highest quality habitat is occupied. But, as density increases, the relative quality of the habitat decreases, until a point is reached at which another habitat type is of equal quality. During the first two winters of this study, when density of sparrows was low, above-average numbers of Sage Sparrows were limited to transects with inkweed. In the subsequent 2 years, densities increased and above-average numbers of sparrows were found on one transect not having inkweed in each winter. During the fifth year of the study, when sparrows were most abundant, above-average densities of Sage Sparrows occurred on four transects that did not have inkweed. Despite the fact that the total sparrow population increased by almost 60% between winter 1978–79 and winter 1979–80, the average density on transects with inkweed remained about the same. Thus, the "excess" birds in the population in 1979–80 were using portions of the habitat that had not been selected when the population was lower.

Whether habitat selection by wintering Sage Sparrows is based on food, vegetation structure or some other resource, it is apparent that the sparrows prefer vegetation with inkweed as a significant component. Presence of Sage Sparrows in areas lacking inkweed appears to be largely restricted to those times when food resource conditions are most favorable (fall and mild winters) or when sparrow numbers are high. Under the more physiologically demanding conditions of winter or generally harsh years, the wintering Sage Sparrow population of the lower Colorado River valley concentrates in areas with relatively high densities of inkweed.

SUMMARY

Overwintering Sage Sparrows (*Amphispiza belli*) were studied for 5 years (1975–1980) in honey mesquite-dominated vegetation of the lower Colorado River valley. Distributional diversity and evenness were reduced between fall and winter of each year. There was also a dietary shift from animal to plant material between seasons. Areas that consistently supported above-average populations had more inkweed shrubs. Results from three sites with controlled vegetation parameters suggest that Sage Sparrows actively select inkweed.

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